How freshwater biomonitoring tools vary sub-seasonally reflects temporary river flow regimes.

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Running head: Biomonitoring tool responses to temporary river flow regimes

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Keywords: Intermittent, ecology, flow cessation, biomonitoring, intra-annual

Abstract

Characterizing temporary river ecosystem responses to flow regimes is vital for conserving their biodiversity and the suite of services provided to society. However, freshwater biomonitoring tools rarely reflect community responses to hydrological variations or flow cessation events, and those available have not been widely tested within temporary rivers. This study examines two invertebrate biomonitoring tools characterizing community responses to different flow-related properties: the 'Drought Effect of Habitat Loss on Invertebrates' (DEHLI) and 'Lotic-invertebrate Index for Flow Evaluation' (LIFE), which respectively reflect community responses to habitat and hydraulic properties associated with changing flow conditions. Sub-seasonal (monthly) variations of LIFE and DEHLI were explored within two groundwater-fed intermittent rivers, one dries sporadically (a flashy, karstic hydrology - TR1) and the other dries seasonally (a highly buffered flow regime - TR2). Biomonitoring tools were highly sensitive to channel drying and also responded to reduced discharges in permanently flowing reaches. Biomonitoring tools captured ecological recovery patterns in TR1 following a supra-seasonal drought. Some unexpected results were observed in TR2 where LIFE and DEHLI indicated relatively high-flow conditions despite low discharges being observed during some summer months. This probably reflected macrophyte encroachment which benefitted certain invertebrates (e.g. marginal-dwelling taxa) and highlights the importance of considering instream habitat conditions when interpreting flow regime influences on biomonitoring tools. Although LIFE and DEHLI were positively correlated, the latter responded more clearly to drying events, highlighting that communities respond strongly to the disconnection of instream habitats as flows recede. The results highlighted short-term ecological responses to hydrological variations and the value in adopting sub-seasonal sampling strategies within temporary rivers. Findings from this study indicate the importance of establishing flow response guilds which group taxa that respond comparably to flow cessation events. Such information could be adopted within biomonitoring practices to better characterize temporary river ecosystem responses to hydrological variations.

Introduction

Temporary rivers are broadly defined as lotic environments that periodically experience flow cessation events and potentially the partial or complete loss of surface waters (Datry *et al*., 2017). Temporary rivers occur in various forms worldwide as a result of both natural (e.g. climate and geology) and anthropogenic (e.g. water resource management operations) controls. Temporary rivers are estimated to comprise at least 50% of the global river network and are projected to become more widespread through future climatic change and societal water demands (Datry *et al*., 2014; 2017). In recent years, a growing body of research has illustrated the high biodiversity supported by transitions between flowing, ponded and dry conditions (Meyer *et al*., 2007; Steward *et al*., 2011; Hill and Milner, 2018), as well as the suite of ecosystem services provided by temporary rivers (Steward *et al*., 2012; Datry *et al*., 2018; Stubbington *et al*., 2018b). Despite this, temporary rivers have historically received limited research attention compared to their perennial counterparts (Leigh *et al*., 2016) and there remains a lack of evidence indicating reliable ways of characterizing ecological responses to flow regime variations in temporary rivers.

A lack of ecological and hydrological evidence available globally constrains the ability to effectively manage river flow regimes capable of supporting healthy riverine ecosystems (Poff *et al*., 2010; Chen and Olden, 2018). As such, there is a growing need to derive robust and spatially transferrable relationships between flow regime properties and ecological responses which can inform how water resources could be balanced to support societal and riverine ecosystem demands (Chen and Olden, 2018). Flow response guilds, defined as groups of taxa which respond to water availability and fluvial disturbance in similar ways (Lytle *et al*. 2017), have been found to reliably characterize ecological responses to hydrological controls (Lytle *et al*., 2017; White *et al*., 2017; Chen and Olden, 2018). Despite this, flow response guilds have rarely been incorporated into biomonitoring practices, which predominantly focus on the sensitivity of taxa to water quality parameters (Carter *et al*., 2006; Bonada *et al*., 2006; Birk *et al*., 2012). This significantly hinders the management and conservation of riverine ecosystems where the water quality of riverine environments may not pose the limiting stressor to

74 aquatic ecosystems, which are instead constrained by other anthropogenic pressures (e.g. flow
75 alterations – Matthaei *et al*., 2010; White *et al*., 2017).

76 Within the United Kingdom (UK), two biomonitoring tools exist which characterize different flow
77 response guilds of aquatic invertebrate communities: the 'Lotic-invertebrate Index for Flow Evaluation'
78 (LIFE; Extence *et al*., 1999) and 'Drought Effect of Habitat Loss on Invertebrates' (DEHLI; Chadd *et*
79 *al*., 2017). LIFE characterizes the preferences of invertebrate taxa to flow velocities and has been
80 historically utilized by UK regulatory bodies (principally the Environment Agency – the environmental
81 regulator of England) to guide water abstraction licencing and track the ecological effects of droughts
82 (Monk *et al*., 2006; Klaar *et al*., 2014). LIFE is calculated by assigning taxa to one of six flow response
83 guilds incorporating 'rapid' flow conditions to 'dry or drought impacted' environments (Extence *et al*.,
84 1999). However, LIFE scores have been found to respond inconsistently to flow cessation events
85 (Chadd *et al*., 2017), particularly when flow velocity preferences of individual taxa may not reflect the
86 hydraulic conditions present during drying events (Wilding *et al*., 2018). DEHLI was developed to
87 address this issue by assigning invertebrate taxa into one of six flow-habitat groups (flow response
88 guilds) typically lost sequentially during flow cessation and drying events based on their ecological
89 preferences (building on the conceptual models and research of Boulton, 2003 and Boulton and Lake,
90 2008 - Chadd *et al*., 2017). However, thus far LIFE or DEHLI have not been widely tested in temporary
91 rivers and it remains unclear how these biomonitoring tools respond to flow cessation events (but see
92 Chadd *et al*., 2017; Wilding *et al*., 2018).

93 Studies examining the ecological structure and functioning of temporary rivers, as well as
94 biomonitoring tools specifically, have typically adopted seasonally targeted sampling programmes (e.g.
95 García-Roger *et al* 2011; Cid *et al*., 2016; Garcia *et al*., 2018; Wilding *et al*., 2018). However, such
96 sampling strategies may not adequately capture temporal trajectories of ecological change occurring
97 within or between different seasons, such as the rapid recolonization of taxa and biological
98 transformations occurring following the resumption of flowing conditions (e.g. Ledger and Hildrew,
99 2001; Bogan *et al*., 2015; Leigh *et al*., 2019) or multiple flow cessation events occurring intra-annually
100 (e.g. Stubbington *et al*., 2016; Hill and Milner, 2018). As such, ecological responses and changes to

biomonitoring tool scores associated with flow regime variations in temporary rivers may not be adequately captured by traditional seasonal sampling strategies. Thus, studies examining short-term ecological responses to hydrological variations, and flow cessation events specifically, are needed in temporary rivers to facilitate a more detailed understanding of ecosystem responses to changing flow regime conditions and the implications this has for biomonitoring programmes. However, examples of sub-seasonal sampling campaigns within temporary rivers are limited globally (rare examples include Davey and Kelly, 2007; Storey and Quinn, 2008; Arscott *et al*., 2010; Stubbington *et al*., 2016; Hill and Milner, 2018) and are even less common for biomonitoring tools (but see Chadd *et al*., 2017). To address this research gap, this study examines how invertebrate biomonitoring tool scores vary sub-seasonally and how this corresponds with community temporal transformations and flow regime variations within two temporary rivers.

Materials and methods

Study area

The sub-seasonal (monthly) variations of biomonitoring tools (LIFE and DEHLI) were explored using two case study temporary rivers in the UK and compared to invertebrate community temporal trajectories and hydrological variations. Invertebrate samples were collected at monthly intervals over a *c.* 1-year period in each case study: the River Lathkill, Derbyshire (December 2011 and November 2012), and the South Winterbourne, Dorset (June 1974 and July 1975; see Fig. 1). The drying patterns within the R. Lathkill and South Winterbourne differ markedly and ecological data was collected during hydrologically dissimilar time periods (see below). As a result, the case studies provide independent opportunities to examine the sensitivity of biomonitoring tools (LIFE and DEHLI) to changes in aquatic invertebrate communities associated with varying river flow conditions and drying events.

River Lathkill

The River Lathkill (and its tributary Cales Dale) was sampled monthly between December 2011 and November 2012 (except October 2012) from 10 sampling locations (Fig. 1a). In total, 96 samples were collected, 26 of which were collected from 3 sites that dried during the study period (the remaining 7

127 flowed continuously during the study period). The environmental characteristics of the study sites and
128 the hydrological conditions within the R. Lathkill prior to and during the sampling period have been
129 detailed elsewhere (Stubbington *et al*., 2016) and are summarised here. The R. Lathkill rises from a
130 carboniferous limestone outcrop and the karstic nature of the underlying bedrock facilitates rapid
131 hydrological responses to individual rainfall events. The fast draining of the underlying aquifer often
132 results in low groundwater levels following periods of low rainfall which causes channel drying along
133 different sections of the R. Lathkill. This is further exacerbated by subterranean anthropogenic drainage
134 networks constructed to transfer water away from historic lead mines, which reduces the water table
135 below its natural level (Wood *et al*., 2005; Ford and Rieuwerts, 2007). Land use across the catchment
136 during the study period was (and remains) predominantly low intensity grazing on unimproved
137 grassland (Stubbington *et al*., 2016). The headwater sites (A-C) typically remain dry for *c*.>6 months
138 annually, while all other sites (D-J, Fig. 1a) flow for longer periods (some of which dry every summer
139 and others dry only during extreme droughts – see Wood *et al*., 2005; Stubbington *et al*., 2016 for
140 further site information). The study period coincided with a significant supra-seasonal drought which
141 affected large parts of central England between December 2010-April 2012 (see Parry *et al*., 2013). The
142 extended drought period caused all study sites to dry for the majority of 2011, until significant winter
143 rainfall triggered the resumption of flowing conditions across all sampling sites during winter 2011-
144 2012. The presence/absence of flow was recorded at *c*. monthly intervals during the study period (Fig.
145 2a), although staff (rangers) within the National Nature Reserve and a water level recorder (maintained
146 by Prof John Gunn, University of Birmingham, UK) also provide regular measurements on the
147 hydrological conditions along the study reaches (Fig. 2b). Such information highlighted that only sites
148 A-C experienced drying events on three separate occasions for *c*. 28, 39 and 46 days in mid-March,
149 mid-May and early-August (2012), respectively (although Site C did not dry during March – Fig. 2a;
150 Stubbington *et al*., 2016). Atypical heavy rainfall and high discharges occurred at several points during
151 the sampling period (Fig. 2b).

152 Invertebrates were collected using three-minute kick samples (using a pond net with a l mm mesh), with
153 sampling effort being divided equally between the mesohabitats present. Specimens were preserved in

154 the field using 4% formaldehyde solution prior to processing and identification in the laboratory.
155 Invertebrate taxa were identified to the lowest practical taxonomic resolution, which was predominantly
156 species level; although Leuctridae, Baetidae, Sphaeriidae, Gerridae, Dytiscidae, Gyrinidae, Planariidae,
157 Zonitiidae and various Dipterans were resolved to family level, while Oligochaeta, Tricladida (non-
158 Planariidae) and Collembola were recorded as such.

159 *South Winterbourne*

160 Monthly invertebrate community samples were collected from 12 locations along the South
161 Winterbourne (Fig. 1b) between June 1974 and July 1975, whereby the total extent of flowing and dry
162 reaches was recorded upon each sampling event (Fig. 2a). In total, 152 samples were collected, 58 of
163 which were collected from 5 sites that dried during the study period. The South Winterbourne is
164 predominantly underlain by a chalk ($CaCO_3$) lithology and drying occurs along the river in response to
165 seasonal fluctuations in the water table (Sear *et al*., 1999). In contrast to the limestone underlaying the
166 R. Lathkill (see above), the chalk provides a highly buffered hydrological response to rainfall events
167 (Sear *et al*., 1999). Landuse across the South Winterbourne is predominantly a mixture of arable
168 agriculture and grassland (NRFA, 2019b), and this has changed minimally across the catchment since
169 the study period (Jon Bass, *Personal observation*). The South Winterbourne exhibits a seasonally
170 variable flow regime, with peak discharges typically occurring between late winter and early spring,
171 before declining over the summer and autumn months (Casey and Ladle, 1976; Armitage and Bass,
172 2013). Temporary sites along the South Winterbourne dried in summer-autumn 1974 (Watkinson *et al*.,
173 1994 – Figs. 2c and 2d), typical of flow cessation events experienced inter-annually along the river and
174 other headwater chalk streams (Armitage and Bass, 2013). The South Winterbourne is one of few rivers
175 regionally which dry within the mid-reaches (most others dry longitudinally downstream from the
176 headwaters – White *et al.*, 2018), which occurs due to inflowing springs and flow augmentation schemes
177 operated in the headwaters by the regional water company (Watkinson *et al*., 1994; Armitage and Bass,
178 2013; Fig. 1b). High nutrient levels within the South Winterbourne (typical of chalk streams regionally
179 – White *et al*., 2018) resulted in a diverse macrophyte community (including *Ranunculus* sp., *Callitriche*

sp., *Rorippa* sp., *Apium*/*Berula* sp.) being recorded along the length of the South Winterbourne during the study period (Watkinson et al., 1994).

Invertebrates were collected *via* three-minute kick samples (as above), with an additional 1-minute hand search being performed on bed features difficult to disturb via kicking (e.g. larger substrates; Murray-Bligh, 1999, ISO, 2012). Invertebrate taxa were identified to the lowest practical taxonomic resolution, which was predominantly species level; although certain Diptera and Coleoptera were recorded at family-level, along with Libellulidae, Notonectidae, Corixidae, Lepidostomatidae Limnephilidae and Leptoceridae, while Oligochaeta, Ostracoda and Cladocera were identified as such. Invertebrate data from the South Winterbourne was recorded in a presence-absence format.

Biological information

In total, four presence-absence matrices (two from each temporary river case study) were examined, with abundance data from the R. Lathkill being transformed to presence-absence to enable direct comparisons with the recording of taxa from the South Winterbourne. For both the R. Lathkill and South Winterbourne, community compositions containing taxa resolved to the lowest practical resolution (respective to each study) was examined ('species-level' dataset). In addition, all taxa comprising each case study were aggregated to 'family-level' (except for those identified to a coarser resolution which were retained in their original format), with both species- and family-level datasets being explored to examine the temporal variations of invertebrate communities at different taxonomic resolutions. The 'Lotic-invertebrate Index for Flow Evaluation' (LIFE - Extence *et al*., 1999) score was calculated for all samples from both case studies at family- (Family LIFE) and species-level (Species LIFE). For calculating the 'Drought Effect of Habitat Loss on Invertebrates' (DEHLI) index, taxa recorded within the species-level dataset were harmonized with the taxonomic resolution required for calculating DEHLI, which predominantly utilizes family-level data but with some/ genus-level classifications (Chadd *et al*., 2017). Lower biomonitoring tool scores indicate changing hydraulic (Family LIFE and Species LIFE) and habitat conditions (DEHLI) as flow velocities and water levels (and associated stages of habitat connectivity) are reduced, respectively.

206 *Data analyses*

207 All statistical analyses reported herein were performed in R studio (operated within R version 3.3.1; R
208 Development Core Team, 2014). Multivariate differences in invertebrate community compositions
209 between monthly sampling periods for both case studies were tested *via* a 'Permutational Analysis of
210 Variance' (PERMANOVA) using the '*adonis*' function in the Vegan package (Oksanen *et al*., 2017).
211 Pairwise PERMANOVA was used to test how communities differed between successive months.
212 'Principal Coordinate Analysis' (PCoA) plots were constructed using a Sorenson dissimilarity index to
213 visualize community differences between months and were performed using the '*cmdscale*' function in
214 Vegan. The correlation between PCoA axis scores and each of the three biomonitoring tools, as well as
215 between each paired combination of biomonitoring tools, were tested *via* the '*cor.test*' function, with a
216 Pearson's correlation coefficient being utilized.

217 Temporal variations of biomonitoring tools were visualized separately for sites which dried and flowed
218 continuously across the duration of each temporary river case study (it should be noted that individual
219 sites are not defined as 'temporary' or 'perennial' to avoid differences in classification and
220 nomenclature established in previous studies – see Stubbington *et al*., 2016). In total, six Generalized
221 Additive Mixed-Effect Models (GAMMs) were utilized to examine how each biomonitoring tool varied
222 spatially and temporally within each case study (i.e. a separate GAMM for each biomonitoring tool
223 within each case study). All GAMMs were fitted using the '*gamm*' function in the mgcv package
224 (Wood, 2017). Each biomonitoring tool (response) was modelled as a smooth function of both time and
225 the distance from the downstream perennial source (km) of each river, which were fitted using cubic
226 splines. Study site was specified as a random effect within all models to reflect the fact that community
227 compositions from individual sites may be correlated over time (Mathers *et al*., 2016). This was
228 determined as the optimal random effect structure in all instances, with pairwise comparisons between
229 each GAMM and a respective model exhibiting the same formula, but without a random effect (also
230 using the *gamm* function) revealing that the former possessed 'Akaike Information Criterion' (AIC)
231 values at least 2 units lower in all instances (Burnham and Anderson, 2002). GAMM outputs were
232 visualized using the '*perspx*' function in the plotrix package (Lemon *et al*., 2018).

Results

Temporal and spatial variations in community compositions

River Lathkill

PERMANOVA highlighted that the invertebrate community compositions exhibited highly significant differences (*p-value* ≤ 0.001) between monthly sampling periods (Family: $r^2 = 0.31$, $F = 3.84$; Species: $r^2 = 0.32$, $F = 3.91$) in the R. Lathkill. Pairwise PERMANOVA testing for differences in invertebrate community compositions between successive months indicated significant changes between February and March (Family: $r^2 = 0.13$, $F = 2.31$, *p-value* = 0.039; Species: $r^2 = 0.16$, $F = 2.77$; *p-value* = 0.003); August and September (Family: $r^2 = 0.28$, $F = 5.51$, *p-value* = 0.002; Species: $r^2 = 0.25$, $F = 4.61$; *p-value* = 0.001) and September and November (Family: $r^2 = 0.20$, $F = 3.57$, *p-value* = 0.027). Principal Coordinate Analysis (PCoA) highlighted clear shifts in invertebrate communities between successive months moving from left to right along axis 1 (explaining 25.07-31.40% of the overall variance) associated with increasing time lapses since the last drying event (and shifts from right to left occurring after drying events in March, May and August; see Fig. 3a). Invertebrate communities inhabiting sites that dried during the study period displayed lower PCoA axis 1 scores, while the sites that flowed continuously exhibited higher axis 1 scores (see Supplementary Material, Appendix A, Fig. A1). PCoA also indicated an increase in axis 2 scores (explaining 17.50-19.82% of the overall variance) throughout the study period in the R. Lathkill. Highly significant (*p-value* ≤ 0.001) positive correlations were observed between PCoA axis 1 scores (for both family- and species-level ordinations) versus DEHLI, Family LIFE and Species LIFE scores, while only DEHLI exhibited a significant (low, negative) correlation with axis 2 scores (Table 1).

South Winterbourne

Within the South Winterbourne, PERMANOVA indicated highly significant differences (*p-values* ≤ 0.001) between monthly averaged community compositions (Family: $r^2 = 0.20$, $F = 2.62$; Species: $r^2 = 0.18$, $F = 2.30$), although this exhibited a slightly lower explanatory power compared to models from the R. Lathkill. Pairwise PERMANOVA highlighted that no community centroids differed significantly

between successive months on the South Winterbourne. PCoA indicated that the summer and autumn months of 1974 were characterised by high axis 1 scores (explaining 21.30-25.07% of the overall statistical variance), although no clear trends were evident in axis 2 scores (explaining 13.08 -14.15% of the overall statistical variance; Fig. 3b). A large shift from right to left along axis 1 occurred between September and October, and community centroids displayed lower and higher axis 1 and 2 scores thereafter, respectively (Fig. 3b). PCoA indicated no clear distinction between invertebrate community compositions inhabiting sites which dried and those which flowed continuously along the South Winterbourne (see Supplementary Material, Appendix A, Fig. A2). Highly significant ($p\text{-}value \leq 0.001$) positive correlations were recorded between PCoA axis 1 values (for both family- and species-level ordinations) versus DEHLI, Family LIFE and Species LIFE scores from the South Winterbourne (Table 1).

Temporal and spatial variations in biomonitoring tools

River Lathkill

For the R. Lathkill, correlations between each pairwise combination of biomonitoring indices were all highly significant (*p-value* <0.001) and highlighted that DEHLI versus Family LIFE (r =0.80, t = 13.21) and Family LIFE versus Species LIFE (r = 0.84, t = 14.77) exhibited strong positive correlations, while DEHLI versus Species LIFE displayed a moderate-strong positive correlation (r = 0.66, t = 8.62). Biomonitoring tool values generally increased within reaches that flowed continuously between winter 2011-2012 and summer 2012, before declining between June and July 2012 and displaying temporally stable values thereafter (Fig. 4a; see Supplementary Material, Appendix A, Fig. A3). Biomonitoring scores were consistently lower at sites which dried compared those which flowed continuously, although DEHLI scores displayed more pronounced differences compared to Family LIFE and Species LIFE (Fig. 4a). In addition, biomonitoring tools (most notably DEHLI) displayed more marked changes between successive months at sites which dried relative to continuously flowing reaches (Fig. 4a). This was particularly evident for March 2012, when all biomonitoring tools displayed a large increase at one site which dried (the other two headwater sites were completely dry at this time – see Fig. 1a) compared to the preceding month (see Fig. 4a and Supplementary Material, Appendix A, Fig. A3). Sites which

dried along the R. Lathkill yielded DEHLI scores that declined substantially between April and May 2012 (but only one of the three sites which dried in the R. Lathkill was sampled in May 2-days before the site dried) and between September and November 2012 (see Fig. 4a and Supplementary Material, Appendix A, Figs. A3a-c). GAMM outputs indicated significant temporal and spatial variations (indicated by the distance from the perennial source) for each biomonitoring tool on the R. Lathkill (Table 2). GAMM outputs highlighted that DEHLI scores from the R. Lathkill sharply increased until spring 2012 and were less variable towards the end of the study period, with values being consistently highest in the mid-reaches (Fig. 5a).

South Winterbourne

Within the South Winterbourne, highly significant (*p-values* <0.001), strong positive correlations occurred between all biomonitoring tools (DEHLI versus Family LIFE - r =0.77, t = 14.97; DEHLI versus Species LIFE - r =0.73, t = 13.11; Family LIFE versus Species LIFE - r = 0.83, t = 18.43). Biomonitoring tools displayed a general decrease between June 1974 and October 1974, and subsequently increased until winter 1975 (Fig. 4b and see Supplementary Material, Appendix A, Figs A3c-e). Family LIFE and Species LIFE were less temporally variable compared to DEHLI (Fig. 4b and see Supplementary Material, Appendix A, Fig. A3f). Samples from sites which dried along the South Winterbourne consistently yielded lower and more temporally variable biomonitoring tool values compared to sites which flowed continuously (Fig 4b and see Supplementary Material, Appendix A, Figs. A3d-f). Some of the highest biomonitoring tool scores obtained from sites which dried occurred in June 1974 (*c*. 2-months prior to channel drying) and January 1975 (*c*. 3-months after channel drying; Fig 4b and Supplementary Material, Appendix A, Figs. A3d-f). DEHLI exhibited highly significant temporal and spatial trends within the South Winterbourne during the study period (Table 2), with DEHLI values notably declining during autumn-winter 1974 and displaying the lowest values within the mid-reaches which dried (Fig. 5b). Although the amount of statistical variation explained by GAMMs was lower for all biomonitoring tools within the South Winterbourne compared to the R. Lathkill (Table 2).

Discussion

Invertebrate community temporal trajectories and correlations with biomonitoring tools

This study provides novel evidence examining how independent biomonitoring tools characterizing invertebrate community responses to different flow-related properties vary in response to hydrological disturbances (channel drying and flow resumption events). Specifically, DEHLI and LIFE (Family and Species taxonomic resolutions) were explored to respectively characterize community responses to flow-habitat and hydraulic properties associated with changing hydrological conditions in two temporary river environments. These biomonitoring tools characterize how invertebrate communities are proportionally represented by different groups of taxa classified by their responses to different flow conditions (i.e. 'flow response guilds' – *sensu* Lytle *et al*. 2017).

The results of this study demonstrate that biomonitoring tools (DEHLI, Family LIFE and Species LIFE) captured the primary forms of community variability (PCoA axis 1 scores) occurring in both temporary rivers. This supports evidence highlighting that biomonitoring tools incorporating information on flow-response guilds can reliably capture temporal trajectories of biotic community change (Vaughan and Ormerod, 2012) and their responses to flow regime variations (Chen and Olden, 2018). This is reinforced by all biomonitoring tools examined in this study displaying lower scores (indicating more hydrologically stressed environments) in reaches that dried compared to those which flowed continuously during the study period. However, it should be noted that previous research has highlighted that other biomonitoring tools characterizing alternative ecological preferences and tolerances (e.g. water quality indicators) display strong differences between temporary and perennial river systems due to the strong deleterious effect that channel drying events can have on aquatic communities (Morais *et al*., 2004; Wilding *et al*., 2018). This suggests care should be exercised when interpreting biomonitoring tools in isolation and that multiple metrics characterizing ecological responses to different environmental pressures should be explored where possible (Clews and Ormerod, 2009; Chadd *et al*., 2017).

Within the R. Lathkill, three headwater sites (of the ten sampled) dried on multiple occasions for *c*. 28-46 days during the study period (Stubbington *et al*., 2016). The temporal variability of invertebrate communities and biomonitoring tools in the R. Lathkill largely reflected these changes in hydrological

conditions. This was most evident in the early stages of the study period, which followed a major supra-seasonal drought that caused all study sites to dry for *c*. nine-months in 2011 (Stubbington *et al*., 2016). Shifts in community compositions associated with increasing antecedent flow durations reflected the (re)colonization of taxa dependent on an extended period of continuous flow, suggesting that ecological recovery took place rapidly during the early stages of the study period. The reduction or partial reversal of ecological recovery in the months following drying events (April, June and September 2012) is in keeping with the limited number of studies that have employed high frequency sampling strategies to examine community responses to multiple drying events occurring intra-annually (e.g. Davey and Kelly, 2007; Storey and Quinn, 2008; Arscott *et al*., 2010; Stubbington *et al*., 2016; Hill and Milner, 2018). Such findings are critical for understanding the resistance and resilience of riverine ecosystems to multiple flow cessation and drying events (Davey and Kelly, 2007; Ledger et al., 2012), which is becoming ever pressing given that such conditions are projected to become more frequent in the future within lotic environments (Wanders *et al*., 2015).

In the South Winterbourne, five sites (of the twelve sampled) located in the mid-reaches of the study area dried on one occasion for *c.* one-five months during the summer-autumn 1974 (although one site also dried in July 1975). Temporal variations in invertebrate communities within the South Winterbourne were not as pronounced as those observed in the R. Lathkill, which probably reflects a greater resistance/resilience of communities to a typical seasonal drying event (Magalhaes *et al*., 2007; Bogan *et al*., 2015) and the presence of upstream perennial sources which allowed invertebrates to rapidly recolonize downstream temporary reaches after flows resumed (Storey and Quinn, 2008; Bogan et al., 2017).

Temporal variations in biomonitoring tools

This study identified strong sub-seasonal (monthly) variations in biomonitoring tools associated with the cessation and resumption of flowing conditions in both case studies. Ecological responses to flow cessation events in riverine environments are often tested through seasonal sampling programmes and/or a space-for-time substitution designs (e.g. control versus impact; Leigh *et al*., 2019). Such study designs and biomonitoring practices may overlook ecological transformations occurring over time

within riverine ecosystems as species are gained or lost, the biotic interactions that stem from this and ecological tolerances to environmental conditions changing over time (Murdock *et al*., 2012; Bogan *et al*., 2015; Leigh *et al*., 2019). This study reinforces the value of adopting sub-seasonal sampling strategies within temporary rivers in order to understand ecological responses to the cessation and resumption of flows at time scales in keeping with the temporal dynamics of ecosystem responses.

In the R. Lathkill, all three biomonitoring tools examined displayed temporal patterns broadly congruent with the temporal transformations of invertebrate communities observed during the study period (see above). This was most evident where biomonitoring tools increased consistently between December 2011 (when flows had recently resumed after a severe supra-seasonal drought) and May 2012, illustrating clear patterns of recolonization and ecological recovery in the R. Lathkill outlined above. Increases in DEHLI, Family LIFE and Species LIFE scores during this time reflects the colonization of taxa with preferences for high-flow conditions ('early colonists' herein) following the supra-seasonal drought (e.g. *Wormaldia* sp. - Philopotomidae, Order: Trichoptera; Rhyacophilidae, Order: Trichoptera; see Supplementary Material, Appendix A, Fig. A4). Biomonitoring tools identified signs of ecological recovery occurring within the mid-reaches of the R. Lathkill, which probably reflects the following two mechanisms. First, early colonists probably resided within the seedbank (life stages that remain viable in the sediments of the riverbed - Tronstad et al., 2005) when the R. Lathkill dried during 2011. Although Stubbington et al (2016) did not record any early colonists utilizing the seedbank across the R. Lathkill during the same study period, it is possible that the thermal or photic cues required for these aquatic insects were not fulfilled (Nordlie and Arthur, 1981) as the authors did not rehydrate the sediments during winter months (when recolonization occurred in the R. Lathkill after the supra-seasonal drought). Second, it is likely that some early colonists sought refuge in adjacent caves and 'soughs' (abandoned, subterranean channels historically constructed to drain water from lead mines - Ford and Rieuwerts, 2007) when the R. Lathkill headwaters dried. These subsurface environments have been found to support extensive aquatic invertebrate communities (Wood *et al*., 2002). Such patterns illustrate the importance of proximal aquatic refuges during drought conditions in facilitating subsequent ecological recovery patterns (Bogan and Boersma, 2012; Hill and Milner, 2018).

In the South Winterbourne, biomonitoring tools responded in synchrony with hydrological variability for most of the study period (Winter 1974 – Summer 1975), with higher DEHLI, Family LIFE and Species LIFE scores indicating invertebrate communities adapted to higher flow conditions and the habitat and hydraulic conditions associated with this (Extence *et al*., 1999; Chadd *et al*., 2017). However, biomonitoring tool scores were notably higher during the early stages of the study period (Summer 1974), despite seasonally low discharges occurring at this time. This suggests that habitat conditions within the South Winterbourne during this low-flow period were suitable for torrenticoles and rheophilic taxa (DEHLI and LIFE), as well as taxa inhabiting marginal regions of the river channel (DEHLI). Various drought tolerant macrophyte species (e.g. *Rorippa nasturtium-aquaticum*, *Berula erectua*, *Apium nodiflorum* and *Oenanthe crocata* – see Westwood *et al*., 2006) are typically most abundant during the summer months in the South Winterbourne (Casey and Ladle, 1976; Armitage and Bass, 2013). Furthermore, surveys conducted during the study period indicated the presence of a diverse macrophyte community across the South Winterbourne during the study period (Watkinson *et al*., 1994). The marginal encroachment of vegetation probably created habitats suitable for torrenticoles and rheophilic taxa (through high flow velocities created between stands - Ladle *et al*, 1972; White *et al*., 2019), as well as species typically associated with streamside vegetation. This habitat complexity associated with macrophytes almost certainly helped maintain high DEHLI, Family LIFE and Species LIFE scores recorded during summer 1974. Comparable findings have been reported previously by Dunbar *et al* (2010), who found that Species LIFE scores responded unexpectedly to hydrological controls within channelized river reaches, with a lack of refugia resulting in lower LIFE scores despite conveying faster flow velocities. Such findings highlight the need for further research to examine how habitat conditions (and specifically macrophyte assemblages) modify how hydrological controls shape flow response guilds and biomonitoring tools derived from this.

Incorporating flow response guilds within biomonitoring practices

There remains a pressing need to understand and model how temporary river ecosystems respond to flow regime variability, including transitions between flowing, ponded and dry conditions, in order to conserve their biodiversity and the suite of services they provide to society. This study highlighted that

biomonitoring tools summarizing different flow response guilds could be more widely incorporated to guide the conservation of temporary river environments (Stubbington *et al*., 2018). To date, flow response guilds have not been widely utilized for examining ecological responses to the cessation and resumption of flowing conditions. Stromberg and Merritt (2016) provide an alternative approach to this by characterizing the ecological guilds of riparian plant communities based on functional typologies associated with ephemeral, intermittent and perennial river systems. Such approaches could potentially be used for characterizing biotic communities inhabiting temporary rivers as the functional properties of biota do not have the biogeographic constraints of taxonomic approaches (White *et al*., 2017, Poff, 2018). This study also highlights that establishing flow response guilds which incorporate the sensitivity of multiple species (which are prevalent across large spatial scales - e.g. nation-wide assessments) to flow cessation events provide a reliable means of deriving ecological associations with flow intermittency.

There are few global examples of biomonitoring tools which incorporate information from flow response guilds beyond the UK (a rare example being the 'Canadian Ecological Flow Index' - Armanini *et al*., 2011). As such, this study provides a unique insight into how different biomonitoring tools established to detect ecological responses to different flow properties perform under extreme hydrological conditions (i.e. channel drying). DEHLI, Family LIFE and Species LIFE were all positively correlated in this research, highlighting the broad associations between hydraulic conditions (LIFE) and flow-habitat groupings (DEHLI) lost during flow cessation events (Chadd *et al*., 2017). This also suggests that invertebrate community responses to hydrological variability, including flow cessation events, can be detected at both family- and species-level taxonomic resolutions (but see Monk *et al*., 2012). However, DEHLI displayed stronger temporal variations compared to Family LIFE and Species LIFE in both case studies and broadly tracked hydrological conditions, most notably within temporary reaches. This provides further evidence highlighting that riverine ecosystems display a stepped response to flow cessation events as key habitats become disconnected within the channel, rather than instream communities responding to a linear continuum of reduced flow velocities (Boulton, 2003; Bogan *et al*., 2015; Chadd *et al*., 2017; Aspin *et al*., 2019a; 2019b).

448 The findings of this research provide valuable insights to help inform future research and management
449 objectives aiming to establish and utilize biomonitoring tools capable of characterizing temporary river
450 ecosystems responses to flow regime variations. Our results suggest that such efforts should target
451 establishing flow response guilds which characterize biotic communities based on their ecological
452 preferences associated with habitats typically available (or lost) at different water levels and flow
453 magnitudes. With temporary rivers likely to become more prevalent due to future climatic change and
454 increasing societal water demands, this study informs the ever growing need to test, develop and refine
455 biomonitoring tools capable of quantifying ecological responses to temporary river flow regimes.

456 **Acknowledgements**

457 We acknowledge the ongoing support of Prof John Gunn on this research and for providing hydrological
458 data for the River Lathkill. Thanks to Thomas Worrall for assistance with the field and laboratory work.
459 We are grateful to Natural England for access permission to the River Lathkill for invertebrate sampling.
460 We extend our gratitude to Mitch Perkins and Andy House for their support on information regarding
461 historic biomonitoring undertaken along the South Winterbourne. We thank two anonymous reviewers
462 for greatly improving the quality of the manuscript.

463 **Data availability statement**

464 Part of the data (from the River Lathkill) underpinning this research are available from the authors upon
465 request. Other data supporting the findings of this study (from the South Winterbourne) are available
466 from the Environment Agency. Restrictions apply to the availability of these data, which were used
467 under license for this study. Data are available from the authors with the permission of the Environment
468 Agency (enquiries@environment-agency.gov.uk).

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Tables

Table 1 – Pearson r correlation tests between Principal Coordinate Analysis (PCoA) axis scores and different biomonitoring tools tested. Stars indicate the degree of significance: NS = non-significant; * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$.

Watercourse	**Biomonitoring tool**	**Family ordination**						**Species ordination**					
		PCOA1			**PCOA2**			**PCOA1**			**PCOA2**		
		R	**T**	***p-value***	**R**	**T**	***p-value***	**r**	**t**	***p-value***	**R**	**t**	***p-value***
Lathkill	**DEHLI**	0.72	10.17	$<0.001^{***}$	-0.31	-3.18	0.002^{**}	0.72	10.03	$<0.001^{***}$	-0.31	-3.21	0.002^{**}
	Family LIFE	0.80	13.11	$<0.001^{***}$	0.05	0.45	0.653^{NS}	0.81	13.39	$<0.001^{***}$	0.02	0.22	0.827^{NS}
	Species LIFE	0.67	8.85	$<0.001^{***}$	-0.02	-0.16	0.877^{NS}	0.66	8.60	$<0.001^{***}$	-0.07	-0.65	0.515^{NS}
South Winterbourne	**DEHLI**	0.62	9.60	$<0.001^{***}$	0.37	4.86	$<0.001^{***}$	0.60	9.17	$<0.001^{***}$	0.16	1.99	0.049^{*}
	Family LIFE	0.51	7.18	$<0.001^{***}$	0.16	1.97	0.051^{NS}	0.52	7.51	$<0.001^{***}$	-0.12	-1.56	0.122^{NS}
	Species LIFE	0.73	13.14	$<0.001^{***}$	0.19	2.31	0.022^{*}	0.73	13.03	$<0.001^{***}$	0.05	0.63	0.530^{NS}

Table 2– Generalized Additive Mixed-effect Model (GAMM) outputs examining the responses of biomonitoring tools to temporal controls and distance from the perennial source. Stars indicate the degree of significance: NS = non-significant; * = $p \leq 0.05$; ** = $p \leq 0.01$; *** = $p \leq 0.001$.

Watercourse	Biomonitoring tool	Model r^2	Time		Distance from perennial source (km)	
			F	*p-value*	F	*p-value*
Lathkill	DEHLI	0.43	4.80	<0.001***	0.93	0.009**
	Family LIFE	0.54	4.94	<0.001***	2.04	<0.001***
	Species LIFE	0.44	1.59	0.002**	2.15	<0.001***
South Winterbourne	DEHLI	0.39	3.04	<0.001***	1.93	<0.001***
	Family LIFE	0.18	4.82	<0.001***	0.27	0.129(NS)
	Species LIFE	0.39	6.03	<0.001***	0.92	0.014*

Figures

Fig. 1 - The location of the two temporary watercourses explored and the study sites therein. a) The River Lathkill (Derbyshire) and b) the South Winterbourne (Dorset). Triangles indicate sites which dried during the study period, circles denote those which flowed continuously and squares denote local settlements.

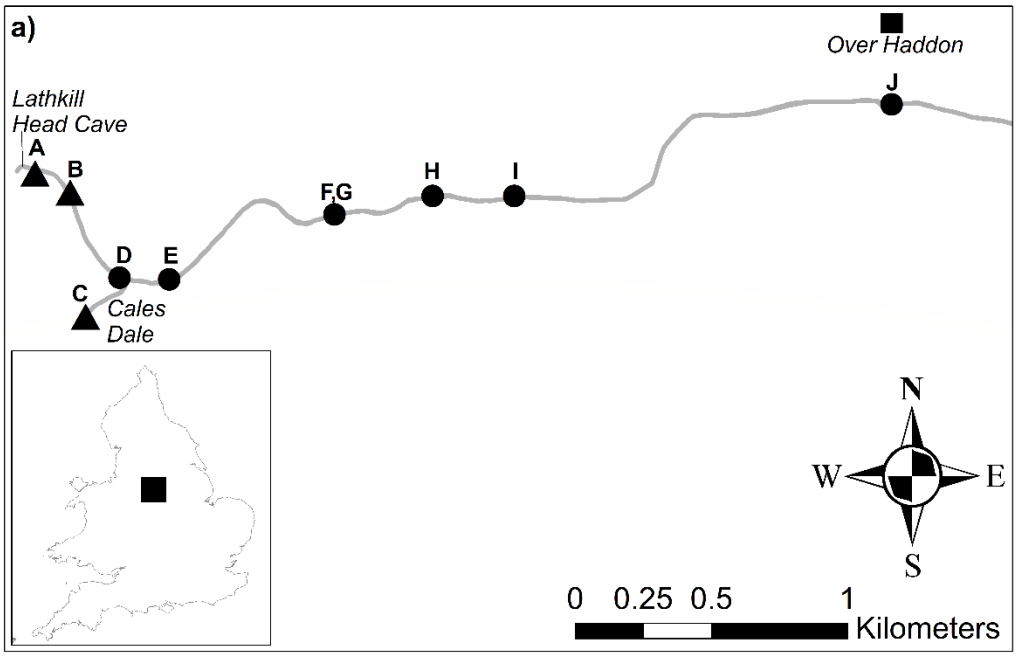
Fig. 2 – Hydrological conditions along the River Lathkill (a and b) and South Winterbourne (c and d) during each respective study period. a) and c) Matrices showing when sites were flowing (grey) or dry (black) for each sampling site (please refer to Fig. 1 for sampling site locations). b) and d) Hydrographs highlighting changes in discharge over time. Note: In d), the black line depicts observed discharges from the South Winterbourne (NRFA, 2019b); while the grey line represents modelled discharges based on a highly significant linear regression ($r^2 = 0.74$, $F = 17604$, $p\text{-value} \leq 0.001$) with discharge time series from a nearby chalk river (NRFA, 2019a) over a 30-year period.

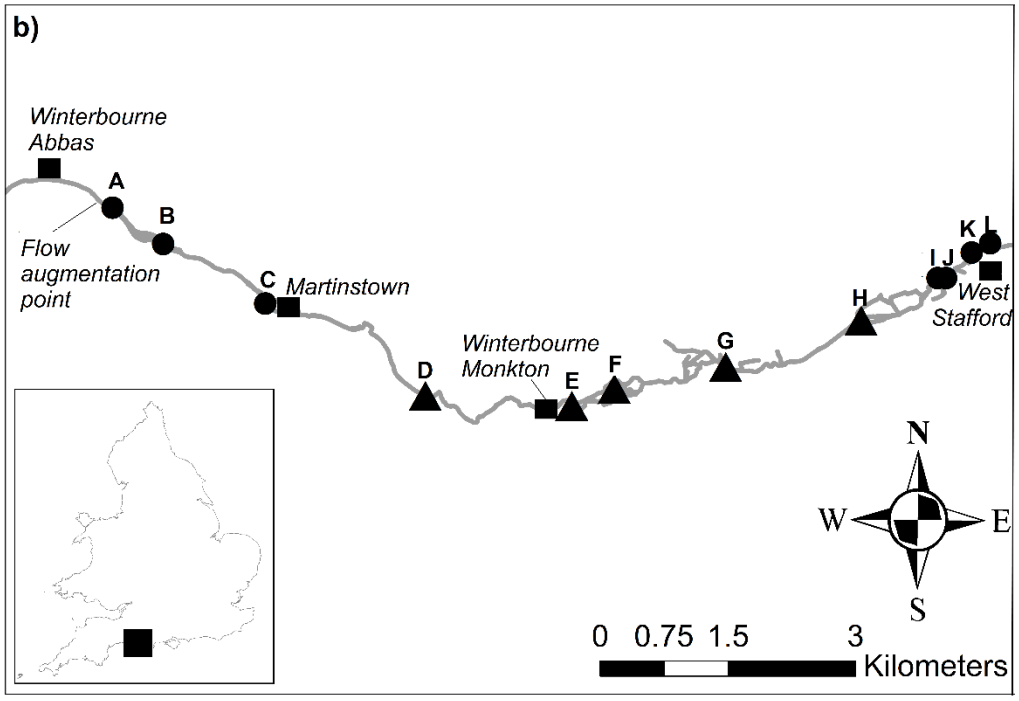
Fig. 3 – Principal Coordinate Analysis (PCoA) plot highlighting average community compositional differences between monthly sampling periods in the a) River Lathkill and b) South Winterbourne.

Fig 4 – Temporal variations in biomonitoring tools (mean ± 2 standard errors) within each case study – a) River Lathkill and b) South Winterbourne. Black = Family LIFE and grey = DEHLI (Species LIFE was excluded for aesthetic purposes due to the high degree of congruency of Family LIFE, but see Supplementary Material, Appendix A). It should be noted that the terms 'temporary' or 'perennial' to avoid differences in classification and nomenclature of study sites established in previous studies.

Fig. 5 – Generalized Additive Mixed-Effect Model (GAMM) outputs highlighting temporal and spatial trajectories of DEHLI scores within each case study. a) Lathkill and b) South Winterbourne. Low to high DEHLI scores are indicated by a gradient ranging from white to black.

780 **Fig. 1**





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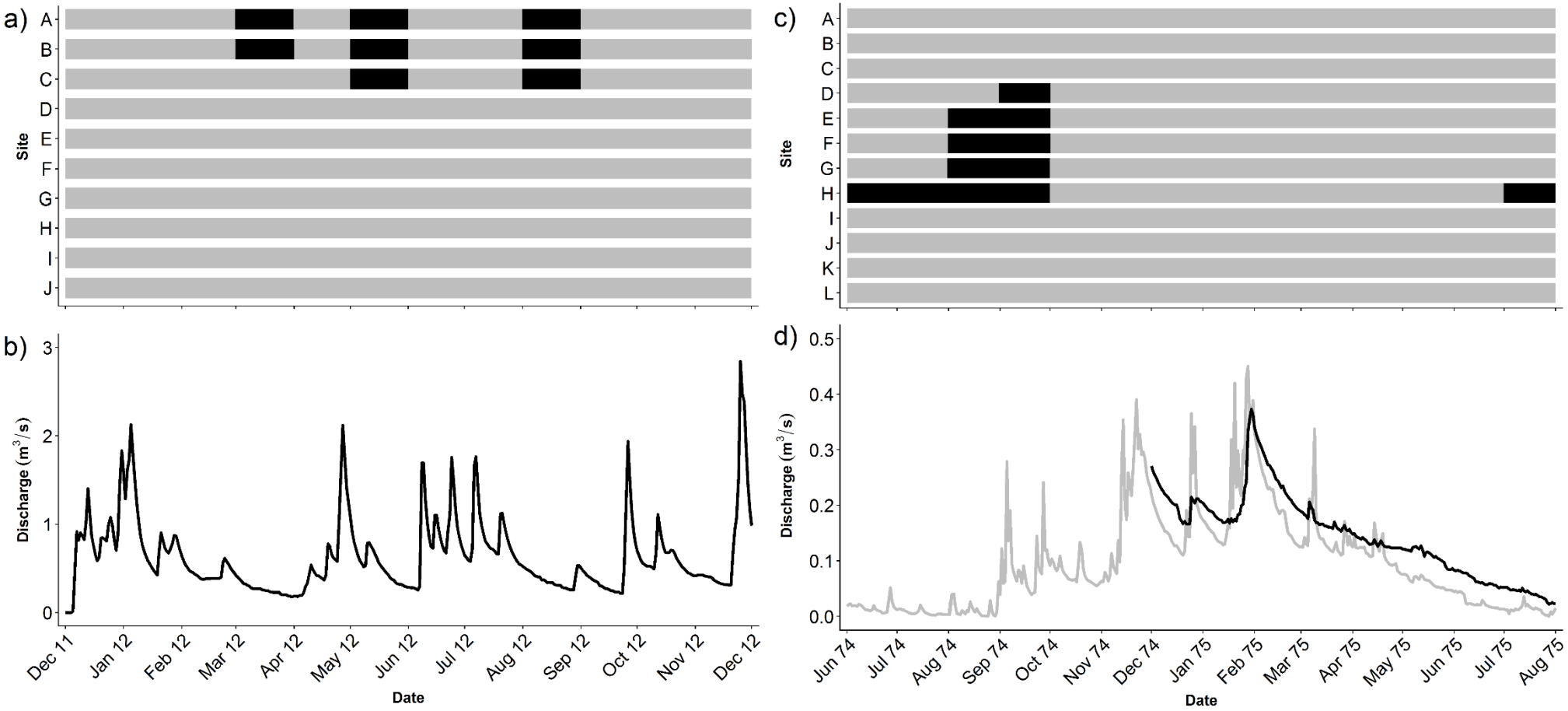
783 **Fig. 2**



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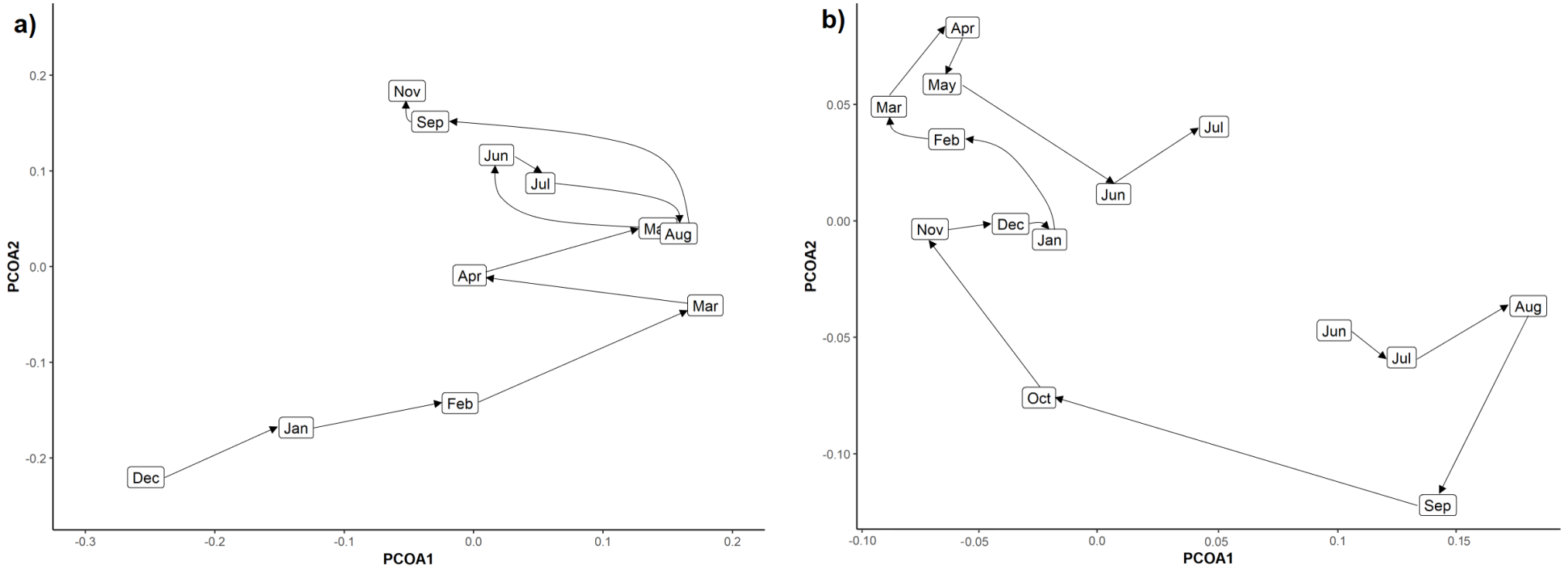
788 **Fig. 3**



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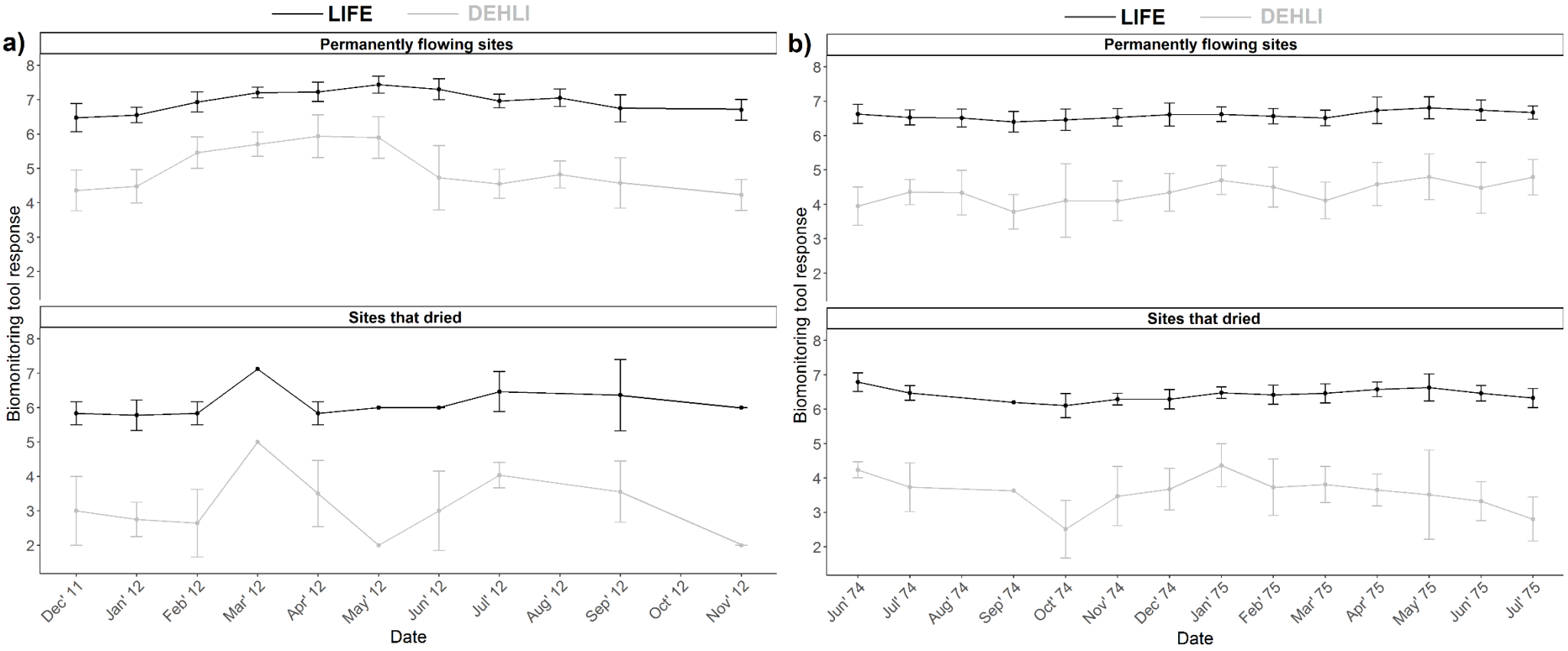
794 **Fig. 4**



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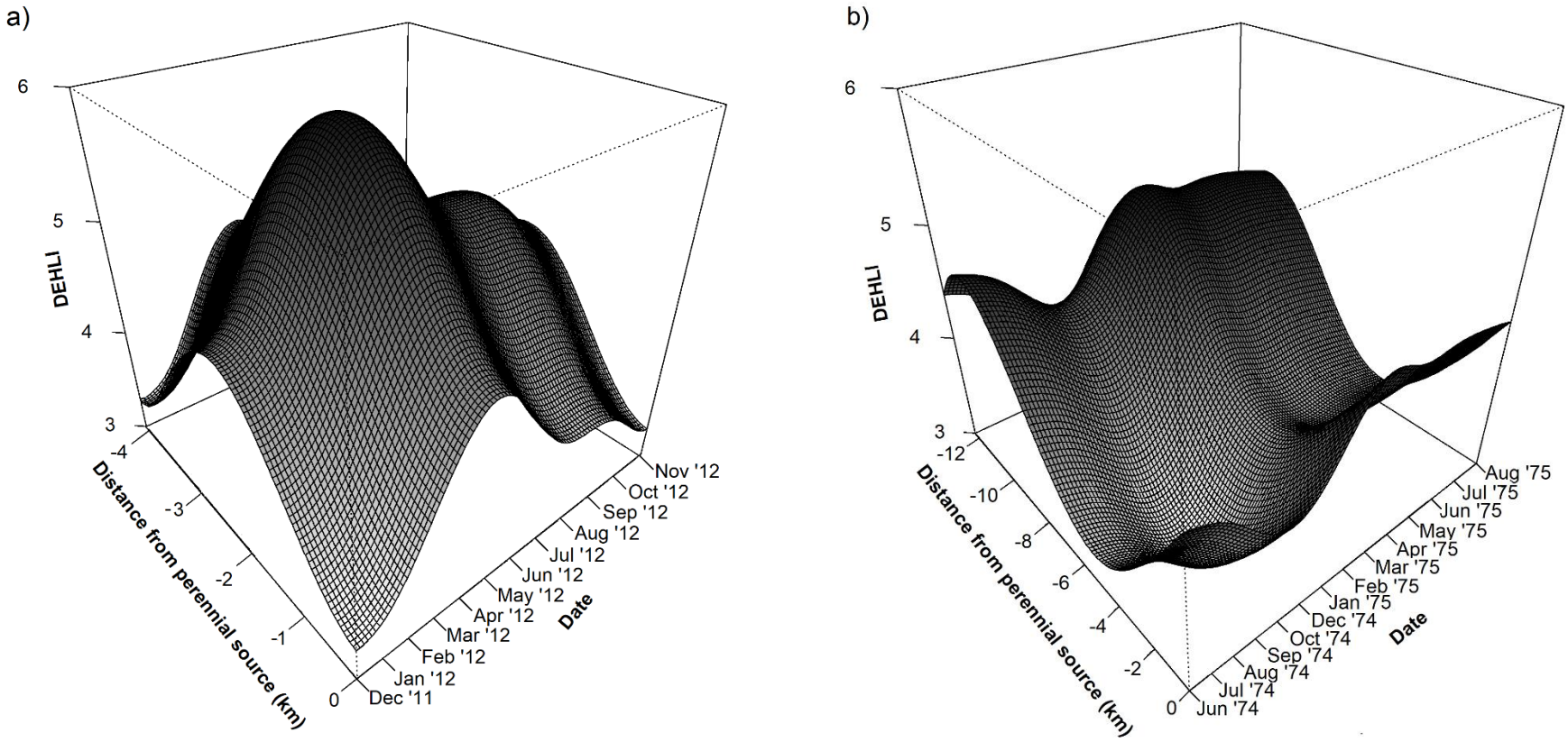
800 **Fig. 5**



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Supplementary material

Appendix A

The following appendix displays additional ecological findings within this study using both multivariate and univariate statistical techniques to assess how invertebrate communities, individual taxa and biomonitoring tools vary spatially and temporally within the River Lathkill and South Winterbourne (the two case studies examined in this study). The three biomonitoring tools are 'Lotic-invertebrate Index for Flow Evaluation' (LIFE - at both family- and species-level taxonomic resolutions) and 'Drought Effect of Habitat Loss on Invertebrates' (DEHLI - the reader is referred to the main text for further details on the case studies and the biomonitoring tools).

Multivariate analyses

Spatial differences in invertebrate community compositions were examined along each of the two temporary watercourses, whereby sampling sites were categorised into one of two 'flow permanence' groups based on whether they flowed continuously throughout the study period (perennial) or exhibited a drying event (temporary). 'Permutational Analysis of Variance' (PERMANOVA) and 'Principal Coordinate Analysis' (PCoA – the reader is referred to the main text for further details on techniques undertaken to perform this analyses) were used to test and visualize community differences between flow permanence groups. Within the R. Lathkill, average community compositions differed significantly (*p-values* ≤ 0.001) between flow permanence groups (Family: $r^2 = 0.20$, $F = 24.13$; Species: $r^2 = 0.20$, $F = 24.13$). PCoA plots highlighted that temporary and perennial sites typically exhibited low and high PCOA axis 1 scores (explaining 31.4% of the overall ecological variance), respectively (Fig. A1).

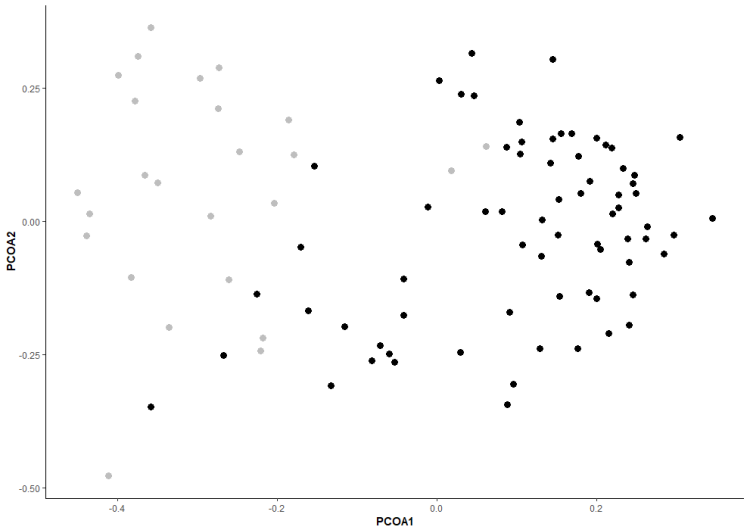


Fig. A1 – Principal Coordinates Analysis (PCoA) plot highlighting average community compositional differences between temporary (grey) and perennial (black) in the River Lathkill case study.

Within the South Winterbourne, average community compositions differed significantly (*p-values* ≤ 0.001) between flow permanence groups, although exhibited a much weaker statistical power compared to the R. Lathkill (Family: r^2 = 0.04, F = 5.73; Species: r^2 = 0.03, F = 4.79). PCoA highlighted a large degree of overlap between invertebrate multivariate compositions exhibited between temporary and perennial sites (Fig. A2).

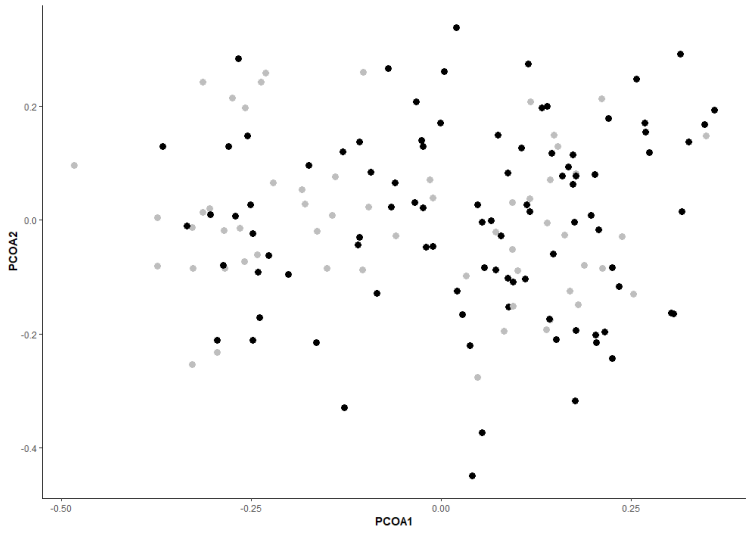
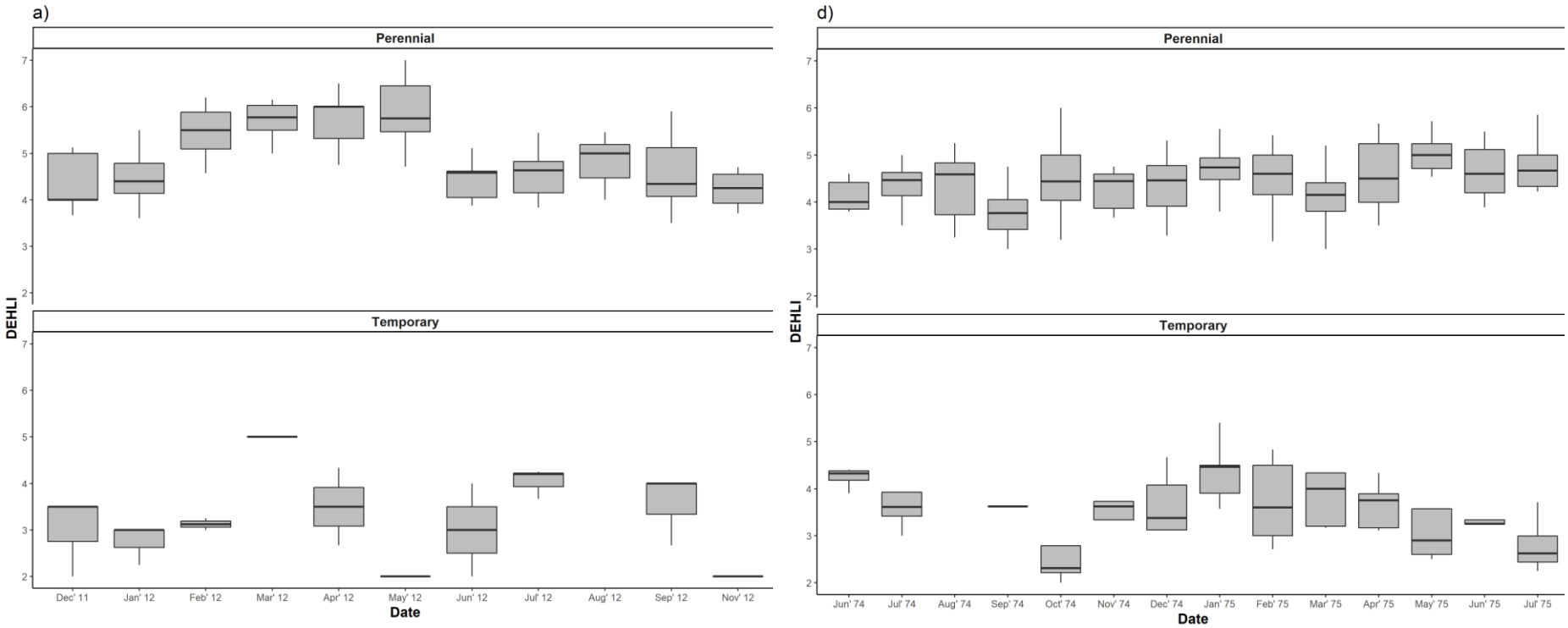


Fig. A2 – Principal Coordinates Analysis (PCoA) plot highlighting average community compositional differences between temporary (grey) and perennial (black) in the South Winterbourne case study.

Univariate analyses

In the R. Lathkill, all biomonitoring tools within perennial sites displayed an increase in values from the beginning of the study period (December, 2011) until May, 2012 and stabilized (albeit with a slight negative trend) thereafter; while responses in temporary sites fluctuated more widely in accordance with hydrological conditions (e.g. drying events in March and May, 2012 – see the main text for further discussion). In the R. Lathkill, DEHLI (Fig. A3a) and Family LIFE (Fig. A3b) displayed a greater degree of temporal heterogeneity compared to Species LIFE (Fig. A3c).

In the South Winterbourne, there was a general decrease in biomonitoring tool values between June, 1974 and autumn, 1974, with values increasing thereafter until winter 1975; this pattern was more accentuated within temporary sites (Figs A3d-e). The remainder of the study period witnessed more stable biomonitoring index values, although DEHLI was more temporally variable (Fig. A3d) compared to Family (Fig. A3e) and Species LIFE (Fig. A3f).


a)
Perennial
Temporary
DEHLI
Dec' 11
Jan' 12
Feb' 12
Mar' 12
Apr' 12
May' 12
Jun' 12
Jul' 12
Aug' 12
Sep' 12
Nov' 12
Date
d)
Perennial
Temporary
DEHLI
Jun' 74
Jul' 74
Aug' 74
Sep' 74
Oct' 74
Nov' 74
Dec' 74
Jan' 75
Feb' 75
Mar' 75
Apr' 75
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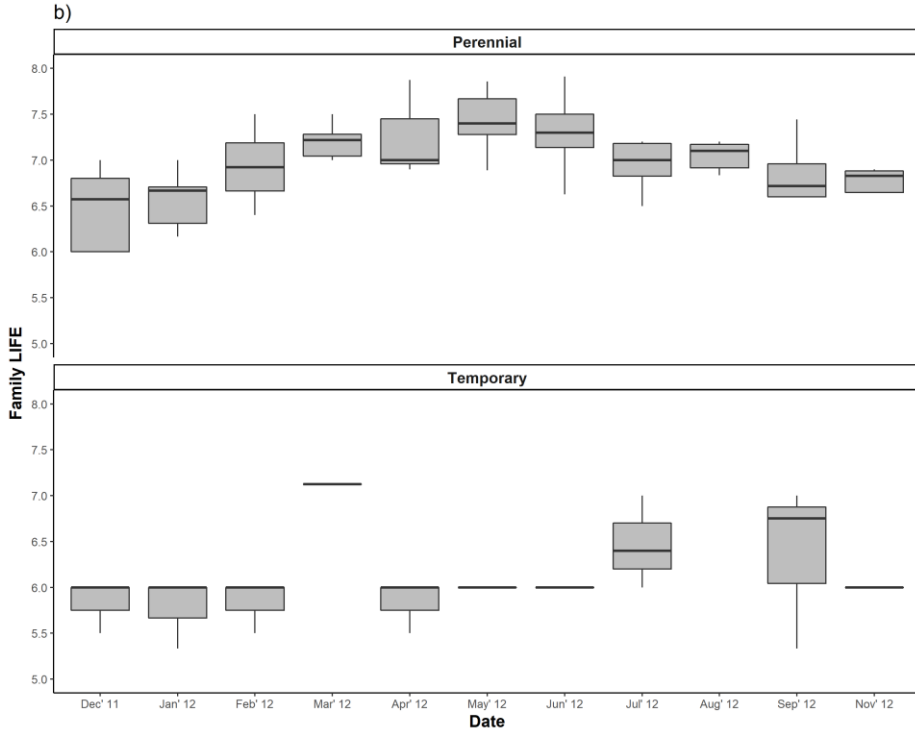
Jun' 75
Jul' 75
Date


b)
Perennial
Temporary
Family LIFE
8.0
7.5
7.0
6.5
6.0
5.5
5.0
Dec' 11
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May' 12
Jun' 12
Jul' 12
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Sep' 12
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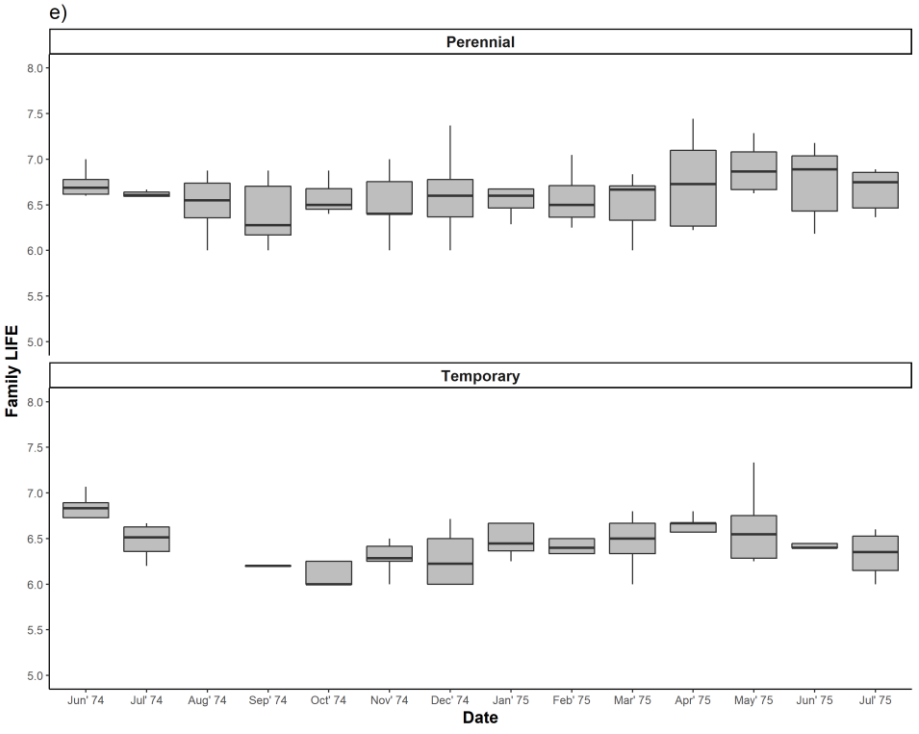
Date


e)
Perennial
Temporary
Family LIFE
8.0
7.5
7.0
6.5
6.0
5.5
5.0
Jun' 74
Jul' 74
Aug' 74
Sep' 74
Oct' 74
Nov' 74
Dec' 74
Jan' 75
Feb' 75
Mar' 75
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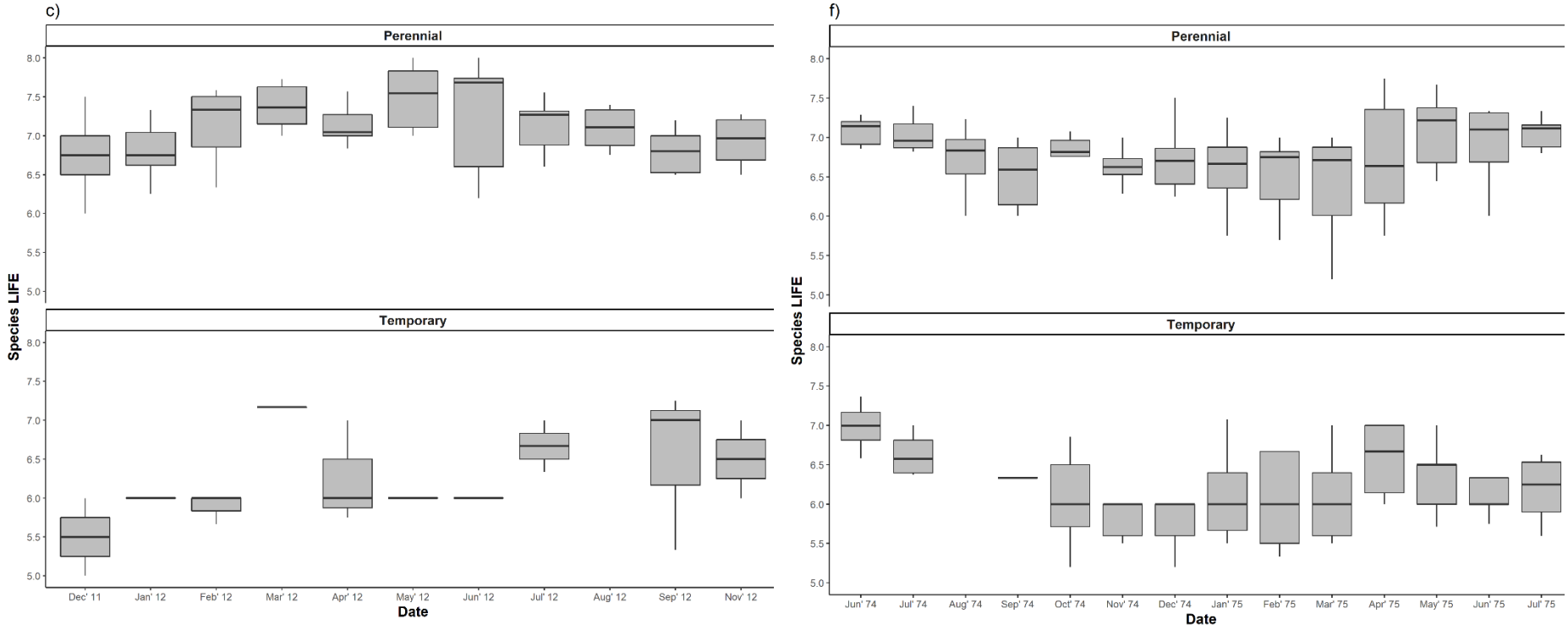
May' 75
Jun' 75
Jul' 75
Date

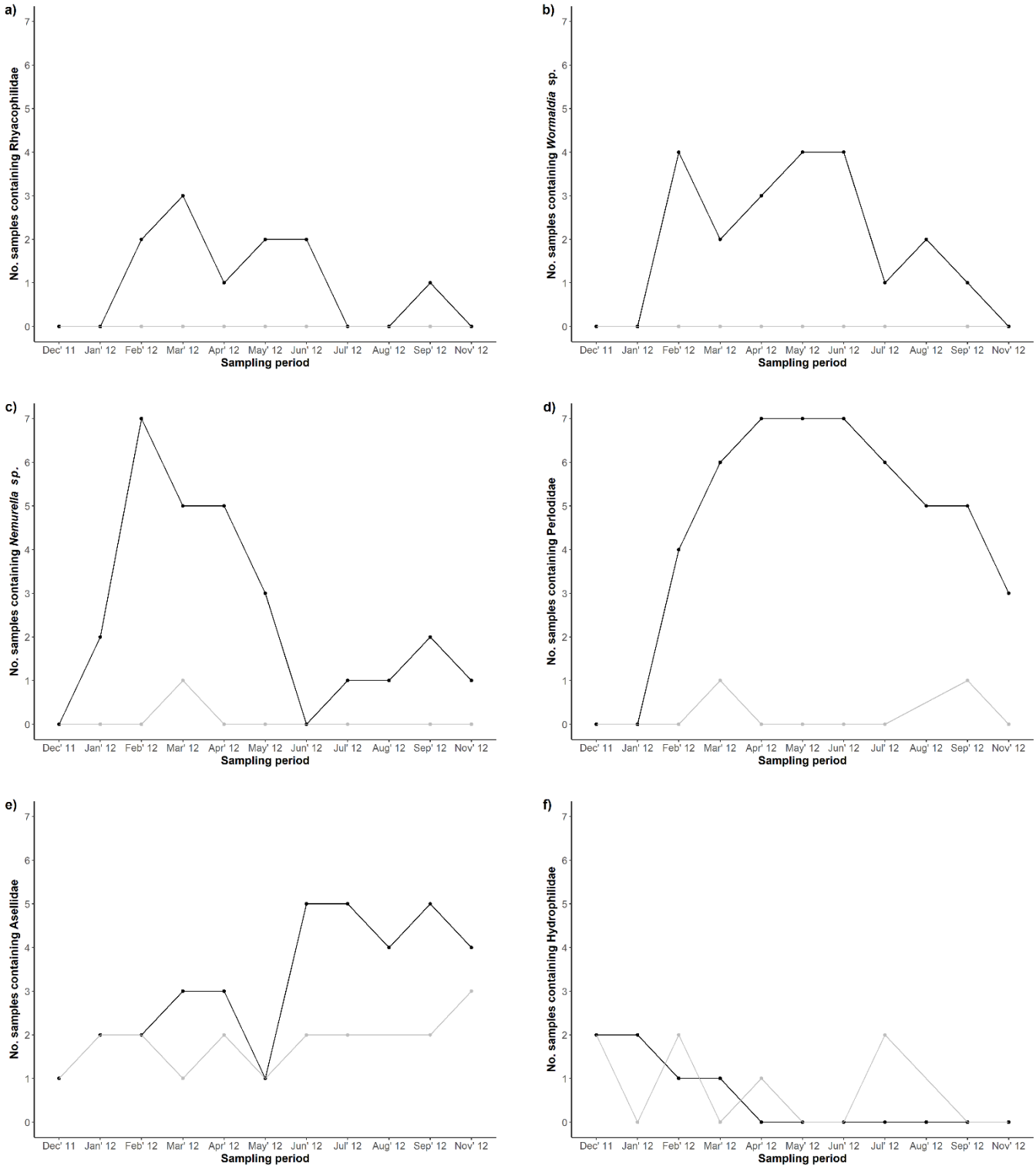


840 **Fig. A3** – Boxplots highlighting differences in biomonitoring index values between monthly sampling periods from the Lathkill (a, b and c) and South
841 Winterbourne (d, e and f) case studies. a) and d) DEHLI; b) and e) Family LIFE and c) and f) Species LIFE. Boxes show the 25th, 50th and 75th percentiles,
842 whiskers indicate the minimum and maximum values within 1.5 times of the interquartile range (for aesthetical purposes, outliers beyond this limit have been
843 removed).

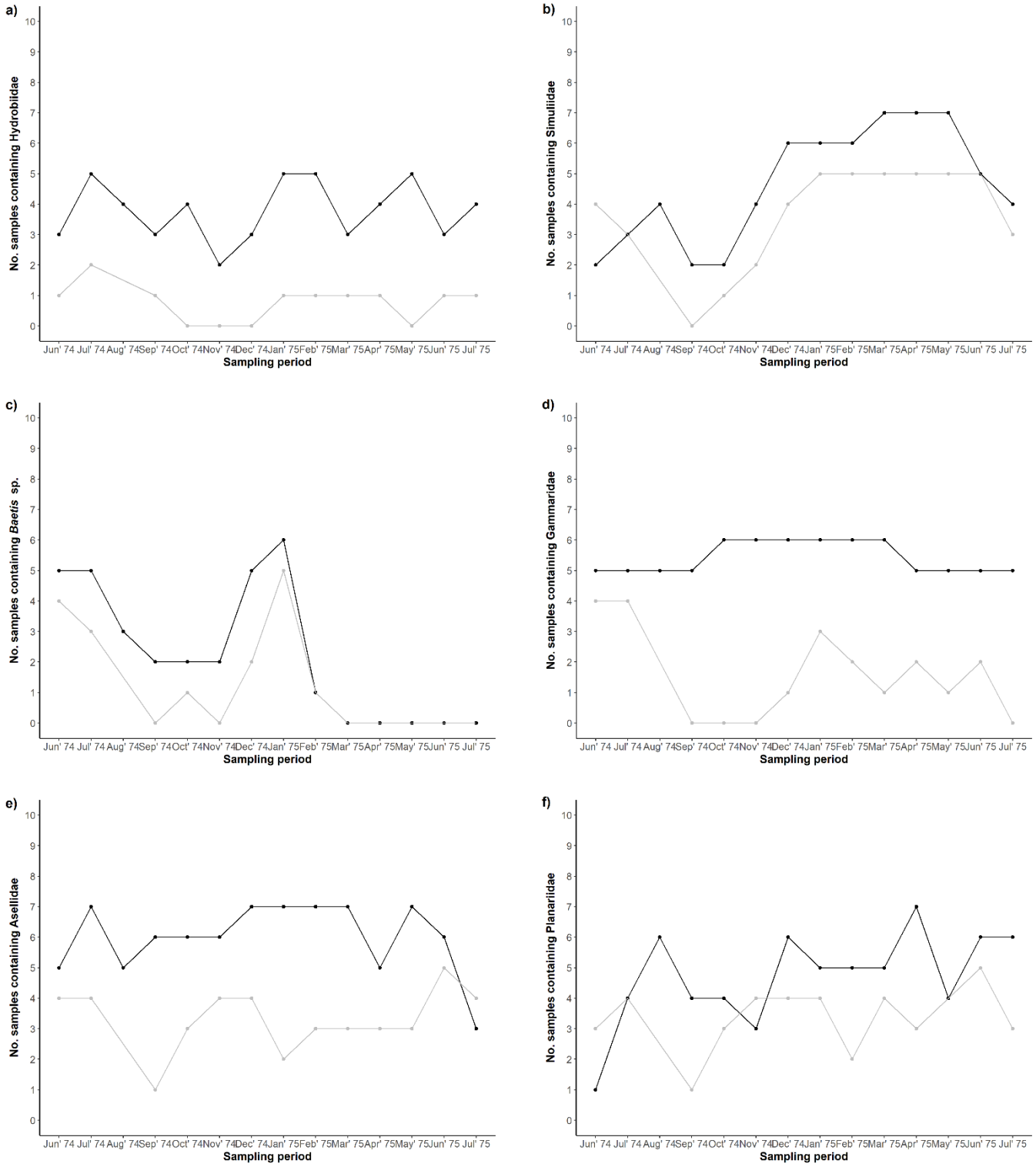
Herein, the temporal variation of taxa individual taxa are described and reported at the taxonomic resolution specified within the DEHLI calculation (i.e. primarily family-level, but with some genus-level classifications) in order to provide some context on the underlying taxonomic responses underpinning variations in biomonitoring tools.

Within the R. Lathkill, certain torrenticoles (e.g. Rhyacophilidae – which contained three species representatives within the *Rhyacophila* genus – Order: Trichoptera and *Wormaldia* sp., Order: Trichoptera) began to establish across perennial reaches between February-June, 2012 (Figs. A4a-b). Other rheophilic taxa (e.g. *Nemurella* sp., Order: Plecoptera; Perlodidae – which contained one species representative, *Isoperla grammatica* – Order: Plecoptera) displayed similar temporal trends at the beginning of the study period, but with a greater degree of success inhabiting larger sections of the R. Lathkill). Alternatively, certain taxa tolerant of dry conditions (e.g. Asellidae, Order: Isopoda; Hydrophilidae, Order: Coleoptera) were sampled from both temporary and perennial sections even from the beginning over the study period (Figs. A4e-f), after a major supra-seasonal drought occurred.

Within the South Winterbourne, certain taxa typically associated with inhabiting macrophyte communities (e.g. Hydrobiidae - which contained one species representative, *Potamopyrgus antipodarum*, Order: Gastropoda and Simuliidae, Order: Diptera) were sampled from both temporary and perennial reaches during summer, 1974, before declining in the succeeding autumn. It should be noted that within the DEHLI calculation, Simuliidae is recorded as being sensitive to the loss of longitudinal flow connectivity (rather than latitudinal connectivity associated with marginal macrophytes, like Hydrobiidae – Chadd *et al*., 2017), but has been widely associated with different macrophytes, including the marginal macrophyte *Rorippa aquaticum*, which inhabited temporary reaches of the South Winterbourne during the study period. Subsequently, these taxa associated with macrophytes increased across the winter months of 1974-1975 (Figs. A5a-b). Other rheophilic taxa (e.g. *Baetis* sp., Order: Ephemeroptera; Gammaridae – which contained one species representative, *Gammarus pulex* – Order: Amphipoda) displayed similar temporal trends to taxa associated with macrophytes, although exhibited strong declines across spring and summer, 1975 (although *G. pulex* were sampled consistently from perennial reaches throughout the study period - Figs. A5c-d). Specialist taxa tolerant of dry conditions (e.g. Asellidae, Order: Isopoda; Planariidae, Order: Tricladida) were sampled from both perennial and temporary sections of the South Winterbourne at the beginning of the study period, although these taxa were more consistently sampled in the former until winter 1974-1975, but declined in temporary reaches across autumn, 1974 before resurging in the succeeding winter months (Figs. A5e-f).



872 **Fig. A4 -** Number of samples containing specific taxa each month within perennial (black) and temporary (grey) reaches
873 in the River Lathkill. a) Rhyacophilidae; b) *Wormaldia* sp.; c) *Nemurella* sp.; d) Perlodidae; e) Asellidae and f)
874 Hydrophilidae.



875 **Fig. A5** – Number of samples containing specific taxa each month within perennial (black) and temporary (grey) reaches
876 in the South Winterbourne. a) Hydrobiidae; b) Simuliidae; c) *Baetis* sp.; d) Gammaridae; e) Asellidae and f) Planariidae.

877 **References**

878 Chadd, R. P., England, J. A., Constable, D., Dunbar, M. J., Extence, C. A., Leeming, D. J. and Wood, P. J. (2017). An
879 index to track the ecological effects of drought development and recovery on riverine invertebrate communities.
880 *Ecological Indicators*, 82. 344–356.